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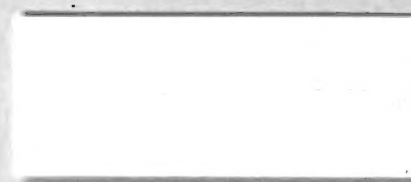
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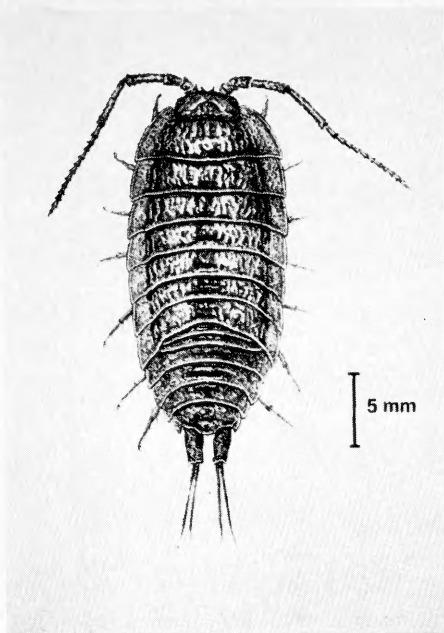
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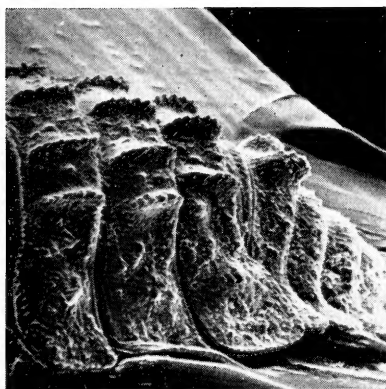
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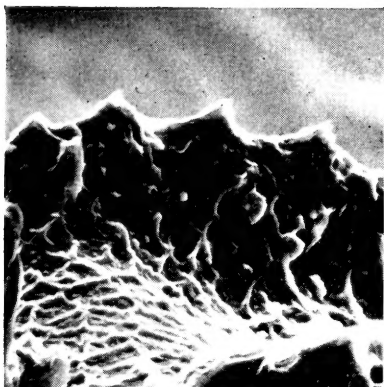


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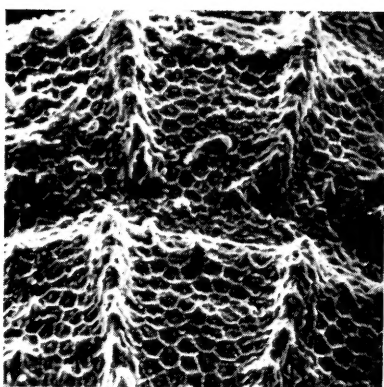


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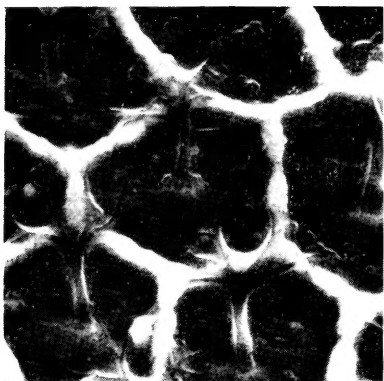
- 1 A terrestrial isopod or woodlouse, *Ligia oceanica* (Linnaeus), family Ligiidae.
- 2 Profile of the rear half of *Haplophthalamus mengii* (Zaddach) as seen with the scanning electron microscope. Magnification  $\times 50$ .



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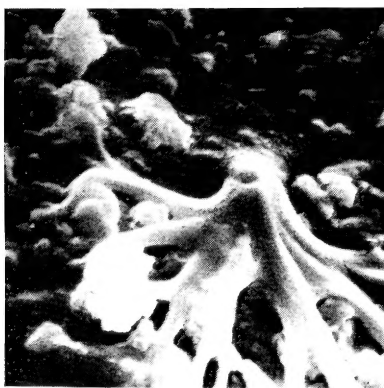
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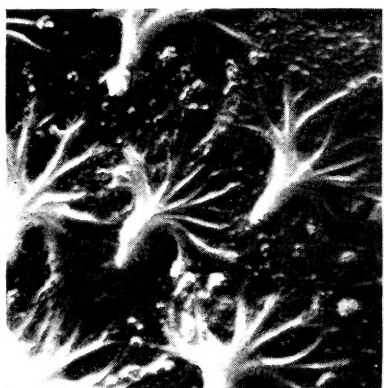
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3 Detail of Fig. 2. Magnification  $\times 520$ .

4 Dorsal surface of *H. mengii* showing polygonal patterning between ridges. Magnification  $\times 160$ .

5 Detail of Fig. 4 showing 'trees' in centres of polygons. Magnification  $\times 1550$ .

6 As Fig. 5, after silver coating. Magnification  $\times 1600$ .

7 Detail of Fig. 6. Magnification  $\times 5500$ .

8 Another individual, after treatment with a decalcifying agent, showing disappearance of the granules. Magnification  $\times 1850$ .

## THE STUDY OF WOODLICE

By S. L. SUTTON

*Department of Zoology, The University of Leeds*

Few animals are so familiar and yet so little known to science as woodlice. We have only the sketchiest knowledge of their ecology and behaviour in the field, even though they occur in remarkable numbers in many habitats, ranging from sand dunes to compost heaps. On this occasion I shall try to persuade you of two things:

- (1) That they are interesting animals;
- (2) That they merit a great deal of further study, not only by professional scientists but by anyone with an interest in natural history.

First perhaps I should explain how I came to be involved with woodlice, since it seems inherently unlikely to most people that anyone should be interested in such animals.

Six years ago I knew nothing about them, but found myself in the curious and perhaps unique position of having a grant to do research and no project. Eventually Mr. Charles Elton of the Bureau of Animal Population at Oxford suggested that I look at a woodlouse that has been common in the grassland on the Wytham Wood Estate nearby, which belongs to Oxford University. In the three years I found three examples of this species *Trachelipus rathkii* (Brandt)—hardly sufficient to sustain an ecological project. However, I did find several other species in some abundance, and was able to carry out a field study of their population ecology. This work made me realise how much there was to find out about the group, and I have had a growing interest ever since.

Given the general nature of my title I could range very widely over the fields of behaviour, morphology, taxonomy, ecology, genetics, physiology and even folklore; but to keep within reasonable limits I must be very selective and have chosen to concentrate on four very different aspects:

- (1) main features of morphology and life history;
- (2) ecology;
- (3) recent discoveries concerning the fine structure of the cuticle;
- (4) The Isopod Survey Scheme now being set up.

I shall introduce these topics within the framework of a systematic review of the more interesting species.

Perhaps I should begin by emphasising that woodlice are Crustacea of the order Isopoda, with many marine and some freshwater relatives. The most primitive British woodlouse is the sea slater, *Ligia oceanica* (Linnaeus). This is also the largest species, adults reaching a length of 30mm. It lives mostly on rocky and cliff-bound shores, just above the high-water mark and in many respects it still has one foot in the sea, whence all woodlice came. Invasion of land by marine isopods may have been up the open shore or via estuarine and fresh-water systems; but in either case the evolution of limbs for walking on the sea bottom enabled them to invade the land more easily—with some muscular development the limbs were able to keep the body clear of the ground and therefore allowed greater mobility. In the same way the development of a brood pouch in which the young could grow until able to fend for themselves was probably an essential prerequisite to the invasion of land, for it allows the young to develop in a watery environment and thus they are protected from desiccation, which is the greatest danger faced by terrestrial organisms. Woodlice have never evolved certain

morphological features found in the more advanced terrestrial invertebrates like the insects and spiders. In particular they do not have the waterproof integument possessed by these animals, so to avoid desiccation once hatched from the brood pouch, they have evolved elaborate behaviour patterns which keep them in damp environments. For example they avoid light (dark and damp go together), have a positive attraction to moist places and a love of narrow crevices where evaporative water loss will be minimal. These behavioural reactions ensure survival on land, but seriously limit the extent to which woodlice can exploit the terrestrial environment, since they are always having to dive for cover when the humidity falls. Nevertheless they have managed to exploit many of the damper niches on land very successfully and are an important component of the fauna in many habitats. One species even inhabits the Algerian desert, spending the hours of sunshine at the bottom of a deep burrow, where the temperature is low and the humidity high. It is said to be active in daytime as well as night, coming out when the sun is hidden and scuttling for cover as soon as the clouds pass.

With regard to anatomical details, *Ligia* (fig. 1) will serve as a model for all terrestrial isopods. The body has three regions—head, pereon and pleon, with seven pairs of walking limbs on the pereon, which is the main part of the body. The head bears two pairs of antennae (the first pair vestigial) and a pair of eyes. The mouth parts are well developed and surprisingly insect-like. At the other end of the body the pleon has limbs modified as flat plates (pleonites) for respiration and (in the male) as external genitalia for sperm transfer, while the final pair form the uropods. Dorsally, the body is heavily armoured, the cuticle being impregnated with calcium carbonate, and each dorsal plate extends laterally to form epimera which give woodlice their characteristic oval shape.

Closely related to *Ligia* is the much smaller species *Ligidium hypnorum* (Cuvier), which is a very active and agile animal, being lightly built without strong epimera or heavy armour. It is obviously related to *Ligia* in having many segments to the flagellum of the antenna, and is most common in marshy ground in the south and east of England.

Members of the extensive family Trichoniscidae are also lightly built and structurally primitive. They are mostly very small and some are quite difficult to identify. *Trichoniscus pusillus* (Brandt) (up to 4.5mm in length) is the best known species, being certainly our most abundant woodlouse, occurring all over Britain and at densities of up to 8000/m<sup>2</sup> in ungrazed limestone grassland. This was the species on which I based my ecological studies in Wytham Woods, its abundance making it very suitable for quantitative fieldwork. I was interested in following changes in numbers and population structure through the years, and trying to identify the factors influencing these changes. My main source of information was a sampling programme involving the extraction of animals from soil cores taken from the study area every month. By examination and measurement of the beasts obtained I was able to follow the progress of the generations through maturity and reproduction to their final disappearance, while pitfall traps gave me information on seasonal activity and dispersal. One of the most interesting findings was that in the drought summer of 1964 (the second driest on record in that area) *T. pusillus* migrated deep into the soil where the humidity was higher, and thereby escaped the fatal effects of desiccation. This behavioural response is clearly of vital importance to the species, and occurs during other adverse conditions such as winter frosts. As no palatable food was available during the drought either in the litter or the soil, all growth ceased, with the result that there were practically no adults to breed in the following spring (normally the peak period of repro-

ductive activity). The drastic fall in reproduction which resulted would have been just as serious for the population as mass mortality in the drought if breeding activity had not risen to a high level in the next few months instead of falling away as in a normal year. As a result the production of young for the year as a whole was fairly good and this, coupled with relatively good survival of the progeny, led to a full recovery in population size within twelve months of the drought. This resilience in the face of environmental adversity was one of the most striking features of this woodlouse population, and is of general ecological interest, as it shows one method by which animals can minimize the effects of fluctuating environment.

I have made this ecological digression to bring in one of the fields of study I wished to mention, and keeping still within the framework of my catalogue of species I wish now to turn to another—the fine structure of the isopod cuticle. *Haplophthalamus mengii* (Zaddach) is a rather odd member of the Trichoniscidae which I have only found in soil cores from two localities, one at Wytham and one at Ampleforth in the North Riding of Yorkshire (there are perhaps a dozen likely sites from which I have taken cores but found no sign of it). It is clearly a soil rather than a litter dweller, and is never more than 5mm long, but very heavily armoured. The dorsal plates are thrown into a series of monumental folds like mountain ranges (figs. 2 and 3) while in the valleys between I have found minute sculpturing of remarkable complexity and beauty. At a magnification of  $\times 320$  (fig. 4) polygonal enclosures become visible and further magnification to  $\times 3100$  shows that rising vertically from the centre of each there is a branched structure or 'tree', hitherto undetected and of unknown function (fig. 5).

These photographs were taken with the scanning electron microscope, which is ideal for the job because of its great depth of focus and resolving power. The apparatus forms an image from electrons bounced off the surface of the specimen and the quality of the image depends, in part, on the density of the surface. The woodlouse integument, probably because of its high calcium content, is very efficient in this respect, and good pictures can be obtained simply by spraying the animal with anti-static fluid beforehand, rather than coating with gold or silver as is necessary with most material. However, for really good resolution, we did coat with silver, and these results were most revealing (fig. 6 and 7). The 'trees' have been badly affected by the treatment but the polygon boundaries can now be seen to consist of rows of granules rather than continuous walls and therefore a strengthening function, which was originally suspected, can be ruled out. Their role remains a mystery. To discover something of the chemical nature of the granules and 'trees' one animal was treated with a decalcifying agent (ethylenediaminetetra-acetic acid—EDTA for short) before examination. As can be seen in fig. 8 the granules have quite disappeared, indicating their calcareous nature, but the 'trees' are unaffected. The latter are probably of a chitinous nature, as this is the main substance remaining in the cuticle after EDTA treatment. The function of the granules and 'trees' remains a matter for speculation, but it seems possible that the former are a means of storing or excreting excess calcium, and the latter could have evolved to prevent the surface of the body from coming into contact with soil water, in the same way that aquatic insects use fine hairs to create an aquafuge surface.

I have also been making stereoscan investigations of other woodlice but have found nothing similar to the situation in *H. mengii*, although in such genera as *Porcellio* and *Oniscus* there is a wealth of sculptural detail of great taxonomic potential.

Leaving *Haplophthalamus* and its structural mysteries to further study I revert to my systematic framework and come next to the second animal on which I was working in Wytham Woods. This is *Philoscia muscorum* (Scopoli), a medium sized species (length up to 10mm) easily confused with *Ligidium hypnorum* but found in rather drier habitats. In comparison to *Trichoniscus* it is a hardy animal, and made no migration into the soil during the drought of 1964, seeming able to withstand the dry conditions in the litter. Most accounts state that this animal is found under stones and in forest litter, but in my experience it is more characteristic of ungrazed grassland, hedgerows and the wilder gardens.

Quite closely related to *Philoscia* is *Oniscus asellus* (Linnaeus), a much larger animal which is abundant in gardens, waste ground and dead wood. It is often said to be our commonest and most widespread woodlouse, but I think that *Trichoniscus pusillus* takes the prize on both counts. Whereas *Philoscia* darts away if attacked, or feigns dead, *Oniscus* clings tightly to the substrate and pulls the body down so that the edges of the dorsal plates (the epimera) are flush with the surface. In this position it is very difficult for a predator to gain a purchase on one of the edges and overturn the animal to reach the vulnerable underparts. The same behaviour has been reported in the myrmecophilous species *Platyarthrus hoffmannseggii* (Brandt), which lives as a scavenger in the nests of several kinds of ants and which is occasionally attacked by its involuntary hosts. It is quite small, pure white, completely blind and locally abundant, at least in the south.

I must move on now to the woodlice best adapted for life on land—members of the families Porcellionidae and Armadillidiidae. *Porcellio scaber* (Latreille) and *Armadillidium vulgare* (Latreille) are the best known species, and show the typical features of each family. Both possess pseudotracheae, which are branching systems of air tubes in the flattened ventral plates of the pleon. These tubes originate in each plate or pleonite, from a single pore, so that gaseous exchange takes place with relatively little loss of water through transpiration. The evolution of pseudotracheae was a significant step forward in the colonisation of terrestrial habitats, because it gave greater independence from moist refuges and led to the exploitation of drier habitats such as stone walls and sand dunes. *P. scaber* occurs in both such places, and is also abundant in gardens. It is not a grassland species, except on the coast, but is plentiful in woodland. There it spends the winter sheltering at the foot of a tree, ascending in the spring to browse off the algae (Pleurococcoids) growing on the trunk and lower branches.

The best known member of the Armadillidiidae is *A. vulgare* which is known also as the pill-bug, a name originating from its pill-like appearance when rolled up and also to its use as one, in the days when medicine was practised more in the hope than in the expectation of success. *A. vulgare* is often found wandering about in the sunshine, something not seen in other British species and for which no satisfactory explanation has been offered. Except near the coast, this species is confined to calcareous soils.

Edney (1954, *Synopsis of the British Woodlice*) lists thirty-seven species, but of these only 29 appear to be definitely native, if by this we mean that they have been present for some years and can live out of doors in all weathers. Of the remaining eight species, six are probably aliens more or less confined to greenhouses, one is synonymous with another, and the last, *Armadillidium opacum* (Koch), has not definitely been recorded in the British Isles. This breakdown must remain provisional until we have much more information about distribution and habitat preferences.

To obtain this information I have, with two colleagues, recently set up the

Isopod Survey Scheme. The basis of the scheme is a card on one side of which is a list of species and on the other a list of habitats. The species collected by thorough search of a habitat unit such as a patch of leaf litter or a rotten log are marked on the card along with the habitat category which best describes the 'unit' examined. The information collected will be transferred to punch cards and these will be used in a computer analysis of habitat preferences. They will also be used to construct maps of distribution by arrangement with the Biological Records Centre of the Nature Conservancy at Monk's Wood. To encourage people with no previous experience of the group to participate, we are undertaking the identification and return of any specimens sent to us. Indeed, to ensure accuracy in recording, we are requiring all collectors to send specimens for confirmation until they have built up a reference collection of checked material. Further information, recording cards and instructions, can be obtained from R. J. A. Metcalfe, Trinity and All Saints Colleges, Horsforth, Leeds LS18 5WD.

#### ACKNOWLEDGMENTS

I am grateful to Dr. J. Sikorski of the Department of Textile Industries, Leeds University, for granting me extensive facilities in connection with the Stereoscan work. I must thank Duckworth & Co. for allowing me to reproduce the illustration of *Ligia oceanica* from Webb & Sillem, *The British Woodlice*.

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*Mutilla europaea* L. (Hym., Mutillidae), a strange situation. This morning I was brought a very fresh example of *Mutilla europaea* L. which had just been taken in the foundry of the printing works here. The works is in the middle of the village, and though a small piece of rough grassland adjoins the works near the foundry, with a larger piece of reasonably well-tended grass beyond, I am aware of no bumble bees' nests therein from which the insect could have come; and the beasts are a bit large to be transported like chelifers.—F. D. BUCK, 'Seirottrana', New Road, Tiptree, Colchester, Essex, 21st August 1969.

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*Anthocharis cardamines* L. (Lep., Pieridae) second brood. On 16th August a fresh male *Anthocharis cardamines* L. was seen in the garden here at Tiptree.—F. D. BUCK, 'Seirottrana', New Road, Tiptree, Colchester, Essex, 21st August 1969.

## HOMOEOSIS AND RELATED PHENOMENA IN THE SMALL COPPER BUTTERFLY, *LYCAENA PHLAEAS* L.

By T. S. ROBERTSON, B.SC., F.Z.S., F.R.E.S., M.I.BIOL.

### INTRODUCTION

Examination, over several years, of a number of homoeotic specimens of *Lycaena phlaeas* L., suggested that homoeosis affected certain areas of the wing more frequently than others, and that perhaps it was more common in the male than in the female. The capture of a female butterfly exhibiting homoeosis provided the opportunity to investigate the inheritance of this phenomenon, and also provided the stimulus to bring together as much homoeotic material in *L. phlaeas* as possible, in order to make a comparative study of it.

#### *Homoeosis and Heteromorphosis*

Cockayne collected data on structural abnormalities in Lepidoptera (7), on homoeosis and heteromorphosis in insects (8), and on insect teratology (9). In his paper on homoeosis and heteromorphosis he adopted Bateson's (1, 2) definition of homoeosis, namely as 'a variation, which consists in the assumption by one member of a meristic series of the form and characters proper to other members of the series'. He referred to the use of the word heteromorphosis to describe 'tissues or organs formed before development has been completed, built up of normal cells arranged in an orderly manner, but situated in an anomalous position'. Homoeosis would appear, from these definitions, to refer to a particular class of heteromorphoses.

In insects the antennae, eyes (possibly), mouthparts and walking limbs constitute a homologous meristic series and are subject to homoeosis. Cockayne reviewed, in a number of articles, homoeosis involving substitutions within this meristic series. The wings are also members of a meristic series, and are subject to homoeosis taking on a number of forms reviewed and classified by Cockayne. These involve forewing replacing hindwing, hindwing replacing forewing, substitution of part of forewing by part of hindwing, and substitution of part of hindwing by part of forewing. Cockayne also described a number of examples of Lepidoptera with substitution of one surface of a wing for that of the other surface. Whilst acknowledging that this phenomenon did not conform with Bateson's definition of homoeosis, but fell into the wider group of the heteromorphoses, Cockayne considered it so closely allied to the others that he thought it inadvisable to separate them. It is customary for entomologists to regard these as examples of homoeosis, and this custom is followed in the present paper. No examples of homoeosis involving eyes, antennae, mouthparts or legs have to our knowledge been observed in *phlaeas*, and this paper deals with only substitutions of wing scaling.

### AN ATTEMPT TO STUDY THE INHERITANCE OF HOMOEOSIS

In breeding *Mellicta athalia* Rott., P. W. Cribb (personal communication) had found homoeosis to appear in certain stocks, suggesting a genetic basis for at least some of the cases of homoeosis.

In May 1967, the capture of a homoeotic *phlaeas* female offered the opportunity of testing this hypothesis. As controls, two other females of this species were taken, in the same locality. Each of the three females was placed in a cage

with freshly potted growing food-plant (*Rumex acetosa* L.). When about 100 eggs had been obtained from each, the butterfly was removed. Each stock was subsequently kept separate. In the early stages the larvae were reared on the plants on which the eggs had been laid. As these became exhausted the larvae were transferred to plastic boxes, 12 larvae to each box. (This method of rearing had been used frequently before, with complete success.) Throughout larval life there was a steady mortality in two of the stocks, namely the homoeotic stock and one of the controls. The other control stock had few losses. Eventually 43 female imagines were obtained from the homoeotic stock and 38 female imagines from one of the controls. From the other control stock 39 males and 47 females were reared. None of these specimens exhibited any significant variations. The emergence took place in mid-July and since the species is not normally in the adult stage at this time it was not possible to bring in a wild male to maintain the homoeotic stock. Attempts to inter-breed males of the control stock with the homoeotic stock failed. Pairings in captivity are difficult but not impossible to obtain in this species.

It is reasonable to conclude that the larval mortality fell upon the males in both the homoeotic stock and one of the controls. Since the original parents were captured a few feet apart it seems possible that these two were siblings and shared a genetic weakness which may or may not be associated with homoeosis. Whether this is a simple mutation or a more complex chromosome imbalance cannot be determined. Further breeding experiments of the kind described are desirable, but since homoeosis is of rare occurrence the opportunity is unlikely to recur.

## A SURVEY OF HOMOEOTIC SPECIMENS OF *LYCAENA PHLAEAS*

### Method

By studying the entomological literature, and by writing to museums and collectors, a considerable number of homoeotic specimens of *phlaeas*, or their descriptions, were located. A blank outline of the wing-shape and venation of *phlaeas* was prepared. Where possible, specimens were examined by the author, and the area affected by homoeosis was sketched onto the blank outline, for each specimen. Full data were appended to each sketch. In other cases, a sketch was made from a published photograph or drawing. If the specimen could be located, the sketch was sent to the owner, who was asked to compare the sketch with the specimen, amend it if necessary, and send it back to the author. Where neither of these procedures could be used, a blank outline was sent to the owner of any specimen located, and the owner was asked to complete the sketch and return it. A completed sketch of another specimen was also sent, so that the correspondent could more readily appreciate what was required. The importance of showing the relationship of the homoeotic areas to the venation was emphasised. Since the wing-shape varies from specimen to specimen this might distort the shape of the homoeotic area, and it was explained that this was acceptable.

By these means, a total of 45 specimens (28 true homoeotic and 17 related forms) was drawn, the details being as follows:

Examined and drawn by the author	34
Drawn from a published figure and the drawing checked by the owner	1
Drawn by the owner	10

In addition references to 4 specimens which could not be located were found in the literature (17, 21, 25, 26, 27, 31). These were: two specimens taken by

South in the last century, an American example, also recorded last century, and a female *inaequalis* recorded by Leeds (17) as having been taken in 1938. Thus of 21 recorded examples 17 were located and drawings were obtained.

### *The Descriptive Process*

Considering the frequency with which different areas of the wing are affected by homoeosis, there are two components, the replacement of background colour, and the replacement of spots. The latter can be more clearly defined than the former. Bright and Leeds' classification of lycaenid markings (6) might have been adopted to indicate spots and Cockayne's classification (7) to indicate venation and cells. A disadvantage of using these two different classifications is that Cockayne numbered cells from posterior to anterior, whilst Bright and Leeds numbered spots from anterior to posterior. Therefore the numbering of spots has been made to conform with Cockayne's numbering of cells and venation, i.e. from posterior to anterior. To define wing area more closely, an estimate of inner, middle and outer sections to each cell was adopted (in terms of linear dimension along the nervures rather than in area). This divided the forewing into 39 areas and the hindwing into 33 areas. The relationship between wing areas and marking and the numbering system is shown in a diagram (Figure A).

For each specimen, a note was made of the occurrence of homoeosis in each and any of these 49 wing areas and affecting each and any of the markings (basals, discoidals, submedians and chevrons). If a specimen was affected bilaterally, any area or marking affected on both sides was counted once. When homoeosis affected a nervure, it was taken as affecting the two cells on either side of the nervure. When a spot or mark (particularly the discoidal) encroached on one or more areas, it was counted only as a spot, and not in the area, unless there was some (usually orange) scaling in the anomalous position associated with the spot or mark. In this way, the frequencies with which different spots and areas were affected were measured. The main categories of homoeosis (forewing on hindwing, upperside on underside) were dealt with separately.

### *Analysing the Results*

The specimens were classified into homoeotics and related forms. The dates and places of capture, the sexes of the specimens and the wing areas affected were all analysed to try to detect any definite trends or patterns.

## RESULTS

### *Geographical Distribution*

The 28 true homoeotic specimens were taken from 15 English and Irish counties, as follows:

Surrey 7, Devon 3, Herts. 2, Lincs. 2, Middlesex 2, Somerset 2, with one specimen each from Bucks., Dorset, Essex, Hereford, Hants., Leics., Northants., Yorks., Cork and Kerry. The absence of specimens from the rest of the British Isles reflects the small amount of fieldwork, of the kind which would uncover such variation, which is conducted there. Almost certainly homoeosis occurs freely throughout the British range of the species.

Of the other forms studied, 13 were taken in Surrey, largely because of the activities of a small number of ardent collectors in that county. The remainder came from Berks., Somerset and Kent (one specimen each).

*Distribution in Time*

The first record of homoeosis in British *L. phlaeas* appears to be South's, of a specimen taken in 1881 (25, 26) although a North American specimen was recorded earlier by Nostrand (21). South's specimen was not located for the present study (if it still exists) and the earliest specimen known to be still in existence is Corbett's (Specimen No. 11) taken in 1895. Homoeotics have been taken at intervals up until the present day, and most of the early recorded examples still exist in collections. The other forms studied have generally not been recorded (or if they have been recorded, have been called homoeotics). Apart from Newman's specimen (Specimen No. 43) which is not homoeotic, and perhaps not heteromorphic, the earliest of the other forms examined, a heteromorphic or possibly intersex form, was that of Bull in 1933 (Specimen No. 37).

The details of the years of capture or emergence of the true homoeotic or other forms examined are as follows:

Year	1895	1906	1908	1912	1917	1920	1924	1928	
Homoeotics	1	1	—	1	1	3	1	1	
Other forms	—	—	1	—	—	—	—	—	
Year	1931	1933	1939	1943	1948	1952	1953	1957	
Homoeotics	1	2	1	1	1	1	—	1	
Other forms	—	1	—	2	—	—	1	1	
Year	1958	1960	1961	1962	1963	1965	1966	1967	No date
Homoeotics	1	1	—	1	2	2	1	1	2
Other forms	—	1	2	1	1	—	5	—	1
Totals: Homoeotics 28, other forms 17.									

Totals: Homoeotics 28, other forms 17.

If the month of capture or emergence is examined, it is found that true homoeotics are much more frequently recorded for the early summer months than for the late summer and autumn months. On the other hand, the other forms examined, with two exceptions, came from the late summer and autumn months. The situation is complicated by the fact that in two cases several specimens occurred in one breeding experiment. To avoid giving undue weight to these, they might be classed as individual 'occurrences' rather than as a separate record for each specimen. In the following table the month-by-month distribution of specimens and 'occurrences' in homoeotics and other forms is given.

Month	Homoeotics		Other Forms		Total	
	Specimens	Occurrences	Specimens	Occurrences	Specimens	Occurrences
March	1	1	—	—	1	1
April	3	3	—	—	3	3
May	5	5	1	1	6	6
June	10	10	—	—	10	10
July	1	1	—	—	1	1
August	1	1	2	2	3	3
September	2	2	2	2	4	4
October	3	2	11	7	14	9
No data	2	2	1	1	3	3
Totals	28	27	17	13	45	40

The end of June divides the first generation sharply from later generations of the year. This has been established in unpublished research by the author. The July to October records include second and sometimes third generation specimens, but these cannot be separated by time of emergence. The preceding table can be condensed as follows, and subjected to chi-squared test for significance.

	<i>Homoeotic Occurrences</i>	<i>Other Occurrences</i>	<i>Total</i>
Spring Generation	19	1	20
Later Generations	7	11	18
Total	26	12	38

Chi-squared = 11.25 1 d.f. Significant at the 1% level.

This confirms that the apparent frequency of homoeotics in the spring generation and of the other forms in later generations is not due to chance, but has statistical significance.

The frequency of the other forms in the later months could conceivably be related to the large preponderance of females in this group, compared with the group of true homoeotics. If females were much more numerous than males in the autumn, the result could be preponderance of a variation found mainly in the female. Leeds (18) recorded a preponderance of females in an autumn emergence of *phlaeas* in 1943. A more detailed study of the numbers of the two sexes through the seasons is needed to clarify this point.

It is interesting to note that homoeotics have not been taken in greater numbers in those years (such as 1947 and 1959) when *phlaeas* has been very abundant. Since, however, it is the later generations, in prolonged hot dry summers, that have produced these population peaks, and homoeosis tends to occur in the early summer generation, this can now be seen to be understandable.

#### *Sex, Symmetry and Inheritance*

The 27 underside homoeotics are distributed by sex and symmetry according to the following tabulation:

	<i>Left Side</i>	<i>Right Side</i>	<i>Bilateral</i>	<i>Totals</i>
Males	4	4	4	12
Females	7	3	5	15
Totals	11	7	9	27

These figures do not differ significantly from equality in numbers between the sexes (chi-squared = 0.15 1 d.f.). Neither do they differ significantly from equality of numbers in left side, right side and bilateral homoeotics (chi-squared = 0.89 2 d.f.). The impression that homoeosis was commoner in males than in females, referred to in the introduction, is therefore not supported by numerical evidence.

The other 17 forms were arranged as follows:

	<i>Left Side</i>	<i>Right Side</i>	<i>Bilateral</i>	<i>Total</i>
Males	1	—	1	2
Females	8	6	1	15
Total	9	6	2	17

The difference between the numbers of males and females is significant at the one per cent level ( $\chi^2=8.47$  1 d.f.). The numbers are too small to apply such a test of significance on symmetry. Both males appear to be, on examination, in a different category of variation from the females. The females include several different aberrant forms, but it may well be that eight of them (Specimens Nos. 29, 31, 32, 33, 34, 36, 37, 38) are in fact female intersexes as suggested by Leeds (17) who named them *inaequalis*. Such a conclusion is supported by the data related to specimens 31–35 inclusive. These were reared by Young from a female *radiata* taken in Surrey. About 150 imagines were reared, roughly equal numbers of males and females. However the females included the five specimens figured, one with dark scaling on the upperside of one hindwing, four with orange scaling on one or other forewing underside. The two phenomena appear to be different expressions of the same abnormality, whether genetic or environmental in origin. However, against the theory that these are intersexes it must be said that the males of the same experiment had generally *lighter* orange on the undersides of the forewings than had the females, whereas the abnormal areas on the females are of a *darker* orange than the general background. A careful examination of the scales, using a binocular microscope, is desirable to throw more light on this problem.

The data relating to specimens 6, 26 and 38 are interesting. These are siblings bred in the  $F_2$  generation of a variety taken in Somerset (22). Number 38 seems to be a more extreme example of the same form as those referred to in the previous paragraph, and thus not a true homoeotic. Numbers 6 and 26 were true homoeotics, a male and a female, the former a small, crumpled, distorted bilateral specimen with holes in the wing. About 50 specimens of this brood were reared by Potter and Young, but the stock was degenerate in a number of ways, and most specimens had scale defects giving a greasy appearance. The stock subsequently almost died out, only one larva surviving the winter. The occurrence of two homoeotics and one possible intersex in this stock may be expressive solely of the general degeneracy, presumably genetic, of the in-bred stock, and not of a simple Mendelian effect.

Eight of the true homoeotics were known to be bred specimens, but in all of these cases there is insufficient information on the other members of the broods concerned to comment on whether there is a genetic basis for homoeosis in *phlaeas*. Of the three specimens bred by the author (Numbers 7, 13 and 22) each was the sole homoeotic in broods of under 15 specimens reared. Eight specimens are known to have been captured.

#### *The Wing Distribution of Homoeosis on 27 Underside Specimens*

In all cases the underside forewing pattern was repeated on the underside hindwing. One specimen (No. 28) with upperside forewing pattern on upperside hindwing was considered to be an entirely different variation and was therefore not included in the analysis of underside homoeosis. The wing areas affected are tabulated for each specimen in Table 1 and the wing markings affected are tabulated in Table 2. The numerical totals are also represented diagrammatically (Figs. B and C). In the 27 specimens, 36 wings were affected, for 9 specimens exhibited bilateral homoeosis. The results have been presented in two ways: firstly, counting the number of specimens having particular wing areas or markings affected by homoeosis, whether on one side or both; secondly, counting the number of wings affected, on the assumption that each wing can be regarded as



TABLE 2.—WING SPOTS AND CHEVRONS AFFECTED BY HOMEOISIS

D = discoidal, numbers refer to the spots, D1, D2, D3 the discoids numbered from proximal to distal. 2-7 the submedian series. 2B, the basal spot in cell 2.

Specimen No. & Side	Spots			Chevrans						Total	
	D1	D2	D3	2B	2	3	4	5	6	Spots	Chevrons
1 L										1	0
2 L										1	0
3 L										1	0
4 L										1	1
5 L										0	2
6 L										1	0
7 L										1	1
8 L										1	1
9 L										2	0
10 L										2	1

(Continued on next page)



being an independent occurrence. This latter is clearly not entirely justifiable but examination of the figures shows that whichever method is adopted the conclusions reached are the same.

The following statements can be made:

1. The costal areas of the wing (cells, 7, 8 and 9) exhibit homoeosis in none of the specimens examined. All other areas exhibit homoeosis in at least one specimen.
2. The middle area of cell 3 is most frequently affected, and the frequency of homoeosis declines steadily as one moves further from this area; both laterally across the nervures and radially parallel to the nervures.
3. Although this area is most frequently affected it is not invariably affected. In 16 of the 36 homoeotic wings or in 11 of the 27 homoeotic specimens it is not affected.
4. Homoeosis can occur as a single area in one cell (e.g. specimens 1, 14 and 16) or extending across more than one adjacent cells (e.g. specimens 9 and 11).
5. More frequently, homoeosis occurs in discontinuous patches, sometimes in one cell (e.g. specimen 2), or adjacent cells (e.g. specimen 8) or in non-adjacent cells (e.g. specimen No. 21).
6. Bilateral specimens may be more or less equally affected on the two sides (e.g. specimens 21, 26, and 27) or may be much more strongly affected on one side than on the other (e.g. specimens 20 and 23).
7. Homoeotic areas may be well-defined areas of wholly forewing scaling (e.g. specimen 22) or may be ill-defined, with an intermingling of hindwing and forewing scaling (e.g. specimen 25).
8. When the discoidal cell is affected, the affected area is sometimes in the form of a long narrow wavy strip (e.g. specimens 10, 22 and 24).
9. Outside the discoidal cell, areas frequently occur which are long and narrow, along or parallel to the nervures (e.g. specimens 3, 12, 19 and 24).
10. Elongation of areas in the direction perpendicular to this, i.e. across the nervures, rarely if ever occurs. If the area extends across nervures it also usually extends well radially (e.g. specimen 11). Specimen 9 is the only one where homoeosis extends somewhat transversely rather than radially.

#### *The Heteromorphic and Other Varieties*

Whereas the 27 underside homoeotics form a well-defined group, and the upperside homoeotic (specimen 28) is apparently unique, the remaining 17 specimens do not form a well-defined group of variants. Classification is difficult, but an attempt is made in this way:

Upperside	1 male	(No. 30)
	1 female	(No. 31)
Underside	Hindwings only	(Nos. 39, 40, 44)
	Hindwings and forewings	(Nos. 41, 42, 43)
	(of these all are females except No. 43)	

Specimens with white scaling in an anomalous area:

1 underside female, hindwing only affected (No. 45).

Specimens with darker orange areas on the forewing sometimes extending into the margin and darkening it (possibly intersexes referable to *inaequalis* Leeds).

Upperside	1 female (No. 29)
Underside	7 females (Nos. 32, 33, 34, 35, 36, 37, 38)

The disadvantages of this classification are:

1. It separates specimen 31 from its siblings (Nos. 32–35) when its inheritance suggests that it may be a different expression of the same variation.
2. It places together numbers 30 and 31 which do not really appear to be closely related forms.
3. It includes the perfectly symmetrical specimen 43 with the asymmetrical forms to which it does not appear to be closely related.

Unless and until a greater number of specimens of these forms can be brought together and examined, a really satisfactory classification cannot be attempted.

#### HOMOEOSIS AND HETEROMORPHOSIS IN RELATION TO DEVELOPMENTAL PROCESSES

The determination of the nature of the tissues finally produced by the developing cells is achieved in two ways:

1. By substances produced within the cells themselves, as a result of the successive production of chemical substances (usually proteins) under the control of the chromosomes.
2. By substances produced outside the cells, passing into them by diffusion or active absorption, from surrounding tissues.

The production of wing scales of a particular shape and pigmentation must be achieved by a succession of processes of these two kinds. When scales of a particular type appear in the 'wrong' position, this could occur by either of the two methods—a change in the chromosomes of a dividing cell, passed on to all the daughter cells derived from it; or by a 'leakage' of some external chemical (i.e. external to the group of cells) into an area where it should not have been. Such chemicals are sometimes called 'organisers' and might be enzymes or co-enzymes operating in an enzyme system. The former phenomenon is called somatic mutation. The irregular and discontinuous distribution of the homoeotic areas suggests that homoeosis is not due to somatic mutation. Homoeosis, although affecting limited areas, seems to be a property of the make up of the whole insect. If so, it becomes apparent only in limited areas. What little evidence there is, suggests that homoeosis in this species is not inherited as a Mendelian factor. Two alternative suggestions regarding the passage of external substances (i.e. external to the particular group of cells concerned) might be considered.

1. There is a direct leakage of a substance from the developing forewing to the developing hindwing.
2. There is an internal leakage through the circulatory system of substances which normally influence only forewing scales, but in homoeosis have their influence also on some of the hindwing scales—perhaps because these cells have failed to be influenced by the correct substances for their hindwing position, and so remain free to be influenced by the 'wrong' substance.

A detailed knowledge of the configuration of the developing circulatory system, and of the folds of the developing wing surface, might throw light upon which of these suggestions is the more likely. The author is at present trying to devise a mathematical descriptive model of the processes by which the normal wing pigmentation of the lycaenid underside might be laid down. A survey of homoeosis and heteromorphosis, coupled with a knowledge of developmental sequences, might eventually resolve the causes of these phenomena.

## ACKNOWLEDGEMENTS

It is clear from the data relating to the specimens studied, that co-operation was freely available from the many collectors who gave me access to their specimens or who made drawings for me. I extend my thanks to all of them. Their names appear in the key to the specimens. Many more collectors and museums were approached, and replied that they had no relevant specimens. Their co-operation, and sometimes encouragement too, was appreciated. In particular, my friends Laurie Christie and Les Young made many useful suggestions and lent a large number of specimens. Without their help I could not have undertaken the survey. I am grateful to our editor, Mr. F. D. Buck, for his advice and assistance, particularly in the very considerable task of preparing my illustrations for publication. The librarian of the Royal Entomological Society gave much useful help in providing copies of many of the journals consulted.

## SUMMARY

An attempt to investigate possible inheritance of homoeosis in *L. phlaeas* failed because all the offspring reared from a homoeotic female were females. Twenty-eight homoeotic specimens of *L. phlaeas* were located in collections and the distribution of the homoeotic areas of the wing is described. Homoeosis is commoner in the spring generation than in the later generations, and seems to occur throughout the British range of the species.

Seventeen other aberrant specimens, sometimes called homoeotics, are also described.

Further work is necessary to relate the occurrence of homoeosis and heteromorphism to the developmental processes by which the wing-pattern is laid down.

## LIST OF SPECIMENS

1. Buckler, H. A. 26.v.39. Marefield, Leics. Female. Leicester Museum collection, 577, 1962.  
Homoeosis, left underside forewing on hindwing.
2. —. 5.vi.06. Ivybridge. Male. Christie collection.  
Homoeosis, left underside forewing on hindwing.
3. Young, L. D. 4.vi.57. North Downs, Surrey. Female. Young collection.  
Homoeosis, left underside forewing on hindwing.
4. Hyde, G. E. 12.viii.28. Near Gainsborough, Lincs. Female. Captured. Hyde collection.  
Homoeosis, left underside forewing on hindwing.
5. Perkins, R. C. L. 4.vi.31. Dartmoor. Male. Tring Collection.  
Homoeosis, left underside forewing on hindwing.
6. Potter, N. B. and Young, L. D. x.63. Bred  $F_2$  ex Somersset. Female. Young collection.  
Homoeosis, left underside forewing on hindwing. (Reference: 22.)
7. Robertson, A. S. 23.iv.62. Copse Wood, Middlesex. Bred. Male. Robertson collection.  
Homoeosis, left underside forewing on hindwing. (Reference: 24.)
8. Young, L. D. vi.58. Oxshott, Surrey. Male. Young collection.  
Homoeosis, left underside forewing on hindwing.
9. Craske, P. C. B. 20.ix.52. Hackbridge, Surrey. Female. Captured. R. M. Craske collection.  
Homoeosis, left underside forewing on hindwing. (Reference: 12.)
10. Reeves, F. S. 4.vi.66. Portland, Dorset. Female. Captured. Reeves collection.  
Homoeosis, left underside forewing on hindwing. (Reference: 23 (figured).)

11. Corbett, H. H. 1.ix.95. Doncaster, Yorks. Female. Captured. ex Bright, Marcon and Castle-Russell collections, now in the Tring collection.  
Homoeosis, left underside forewing on hindwing. (References: 7 (figured), 19 (figured) 4, 14, 31, 33)
12. —. Cork, Male. L. Christie collection.  
Homoeosis, right underside forewing on hindwing.
13. Robertson, T. S. 27.vii.65. Chorleywood, Herts. ex ovum Male. Robertson collection.  
Homoeosis, right underside forewing on hindwing.
14. —. Didmarton, Br. vi.20. Male. Siviter-Smith collection.  
Homoeosis, right underside forewing on hindwing.
15. Leeds, H. A. 20.v.43. Hunts. Female. Siviter-Smith collection.  
Homoeosis, right underside forewing on hindwing. (Reference: 18.)
16. Jarvis, F. V. L. v.48. Banstead, Surrey. Female. L. D. Young collection.  
Homoeosis, right underside forewing on hindwing. (Reference: 16.)
17. —. Peterborough. Female. ex H. A. Leeds collection now in Siviter-Smith collection.  
Homoeosis, right underside forewing on hindwing.
18. Stafford, A. E. 9.vi.24. East Sheen, Surrey. Male. Captured. Stafford collection.  
Homoeosis, right underside forewing on hindwing. (References: 8 (figured), 14, 15, 28, 29, 30.)
19. Quibell, W. 23.iv.33. North Lincs. Female. L. Christie collection.  
Bilateral homoeosis and black scaling on one hindwing nerve.
20. —. Bred 30.iii.12. Breinton, Hereford. Male. ex Bessemer collection, now in Tring collection.  
Bilateral homoeosis.
21. Collier, A. E. Bred from egg v.60. Cranleigh, Surrey. Female. Collier collection.  
Bilateral homoeosis. (Reference: 10.)
22. Robertson, T. S. 26.iv.65. Herts  $\times$  Middlesex cross. Female. Robertson collection.  
Bilateral homoeosis.
23. Frohawk, F. W. 1.vi.20. Thundersley. Male. Tring collection.  
Bilateral homoeosis. (References: 8 (figured), 13 (figured).)
24. Sabine, L. A. E. 23.v–17.vi.20. Co. Kerry. Male. Captured. Tring collection.  
Bilateral homoeosis. (Reference: 14.)
25. Robertson, T. S. 28.v.67. Chorleywood, Herts. Female. Robertson collection.  
Bilateral homoeosis.
26. Potter, N. B. and Young, L. D. x.63. Bred  $F_2$  ex Somerset. Male. Young collection.  
Bilateral homoeosis. (Reference: 22.)
27. Quarrington, A. 29.vi.17. Purley, Surrey. Female. Captured. ex Bright and Marcon collections, now in the Siviter-Smith collection.  
Bilateral homoeosis. (Reference: 7 (figured).)
28. Oliver, G. B. 5.x.33. Bucks. Chilterns. Female. Bred. ex Castle-Russell and Marcon collections, now in the Tring collection.  
Homoeosis, right upperside forewing on hindwing. (References: 20, 32 (figured).)
29. Stockley, R. E. vii.60. Surrey. Female. Stockley collection. Orange streaks, darkening the margin, on left upperside forewing.  
Possible intersex *inaequalis* Leeds.
30. Stockley, R. E. 22.ix.53. Surrey. Male. Stockley collection.  
Black streaks on left upperside forewing.
31. Young, L. D. x.66. Bred ex *radiata* stock, Surrey. Female. Young collection.  
Black streaks and blue scales on left upperside hindwing.
32. Young, L. D. x.66. Bred ex *radiata* stock, Surrey. Female. Young collection.  
Orange streaks on right underside forewing. Possibly referable to *inaequalis* Leeds.
33. Young, L. D. x.66. Bred ex *radiata* stock, Surrey. Female. Young collection.  
Orange streaks on right underside forewing. Possibly referable to *inaequalis* Leeds.

34. Young, L. D. x.66. Bred ex *radiata* stock. Surrey. Female.  
Orange streaks on left underside forewing. Possibly referable to *inaequalis* Leeds.
35. Young, L. D. x.66. Bred ex *radiata* stock. Surrey. Female. Young collection.  
Orange streaks on left underside forewing. Possibly referable to *inaequalis* Leeds.
36. —. 15.x.43. Hinchley Wood. J.C.B.C. collection 8060. Female. L. Christie collection.  
Dark marks in margin and orange streaks on right underside forewing. Possibly referable to *inaequalis* Leeds.
37. Bull, G. V. 14.x.33. Sandhurst. Female. L. Christie collection.  
Dark marks in margin and orange streaks on right underside forewing. Possibly referable to *inaequalis* Leeds.
38. Potter, N. B. and Young, L. D. x.63. Bred F<sub>2</sub> ex Somerset. Female. Young collection.  
Extensive orange area on right underside forewing, darkening the margin. (Reference: 22)
39. No data. Female. Siviter-Smith collection.  
Small black streaks on right underside hindwing.
40. Bolton, E. L. 23.ix.61. Surrey. Female. Bolton collection.  
Dark streaks on left underside hindwing. (Reference: 3.)
41. Bolton, E. L. 7.viii.61. Surrey. Female. Bolton collection.  
Bilateral, dark areas on underside hindwings. (Reference: 3.)
42. —. 7.x.43. Hinchley Wood. J.C.B.C. collection. 7940. Female. L. Christie collection.  
Dark streaks and patches on left underside hindwing and darkening of margin of left forewing.
43. Newman, L. W. 1.x.08. Netted Bexley. Male. Tring collection.  
Described in collection as 'ab nov—hindwings and forewing margins sooty, upperside normal'.
44. Bolton, E. L. 6.x.57. Surrey. Female. Bolton collection.  
Described in collection as 'homoeosis'. Dark areas on left underside hindwing.
45. Young, L. D. 18.viii.62. Surrey. Female. Young collection.  
Pale areas on left underside hindwing, not the usual 'pathological' form.

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8, Buckland Avenue,  
Slough, Bucks.  
6th May 1969

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*Plusia gamma* L. (Lep., *Plusiidae*), an exceptional year. Whilst doing a tour of wardening duty on the Colne Point Reserve, near St. Osyth, Essex, for the Essex Naturalists' Trust, 10.viii.69, *Plusia gamma* L. was found to be in exceptionally large numbers. Everywhere on the saltmarsh from Colne Point up to Point Clear the insect rose in clouds as we moved across the marsh. Basil Harley, who was wardening with me, and I estimated a minimum of 100,000 examples on the Reserve alone.—F. D. BUCK, 'Seirotana', New Road, Tiptree, Colchester, Essex, 13th August 1969.

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#### ERRATA

Vol. 2, part 2. The legends 1-12 on Plate IX belong to figs 25-36 respectively on Plate XI, and vice versa. An amendment slip is enclosed with this issue for inserting into this part.

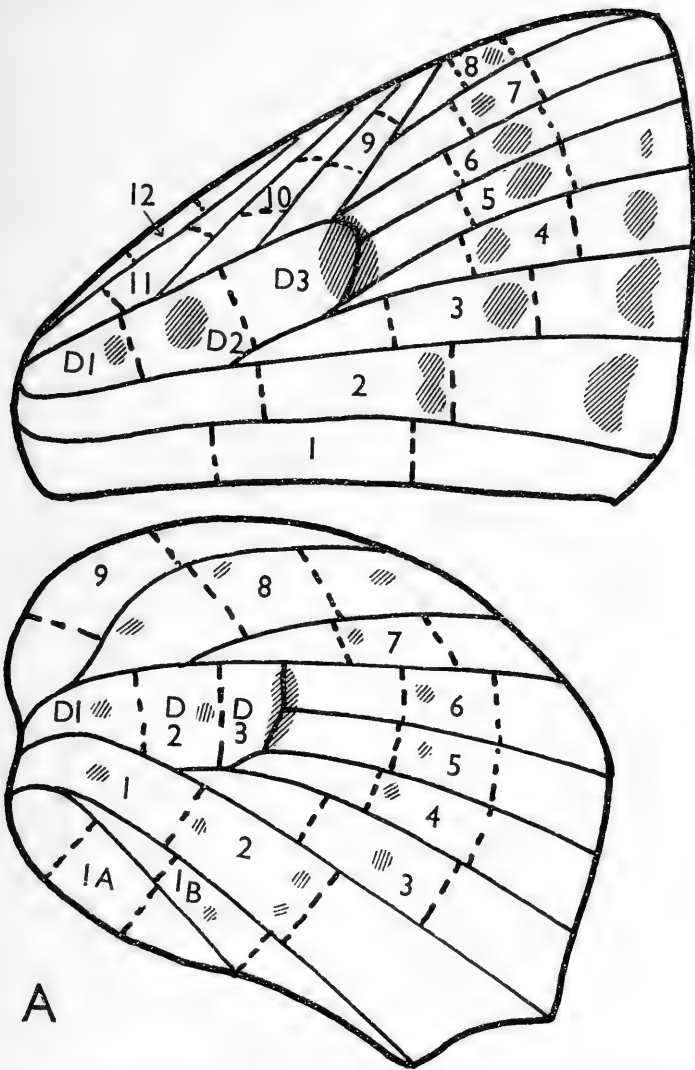
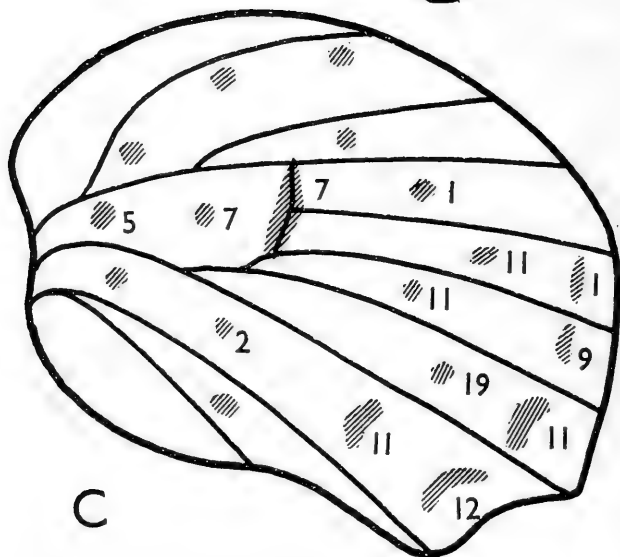
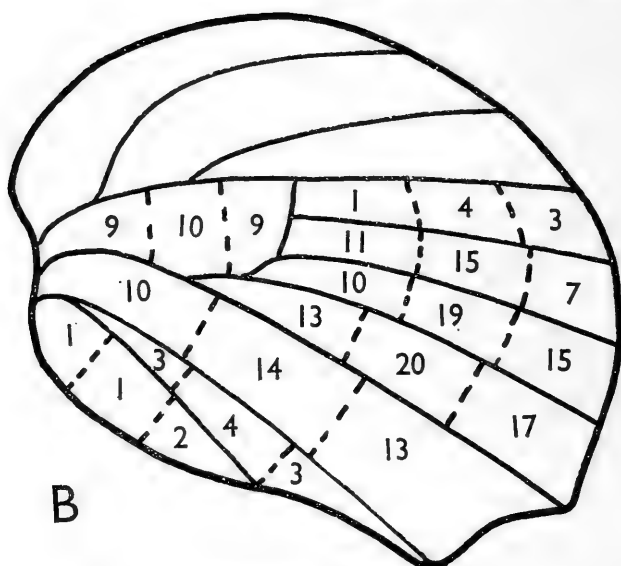
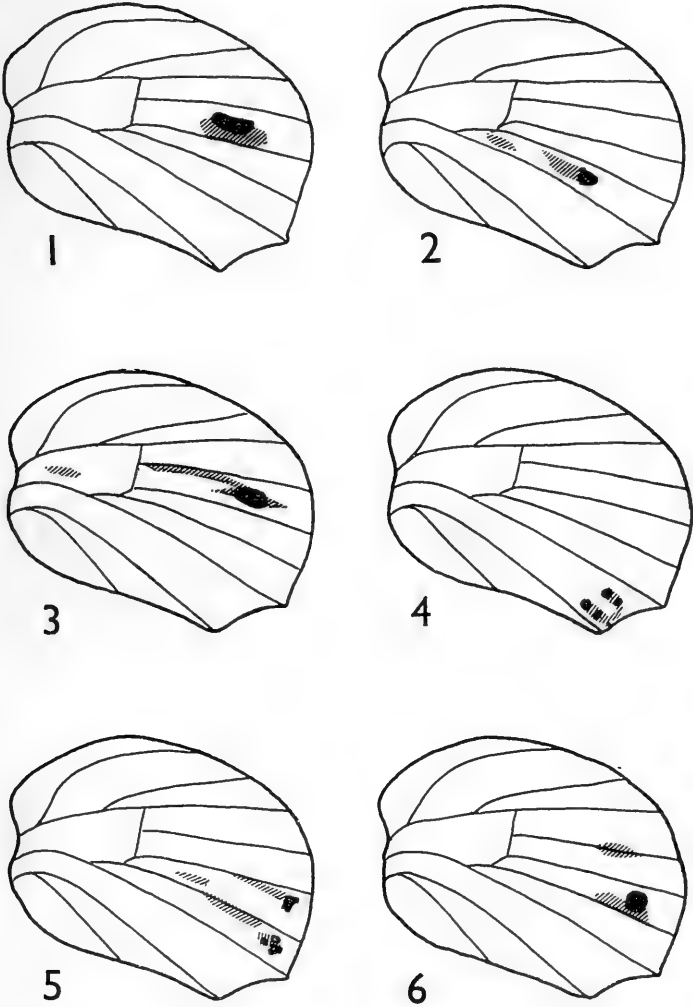


Figure A: Key to wing areas and markings of *Lycaena phlaeas*

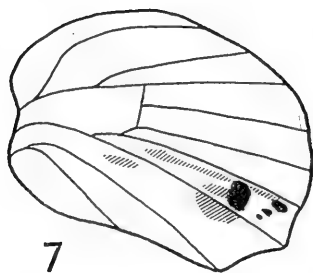


*Figure B:* Frequencies with which different wing areas were affected by homoeosis (27 specimens, 36 affected wings)

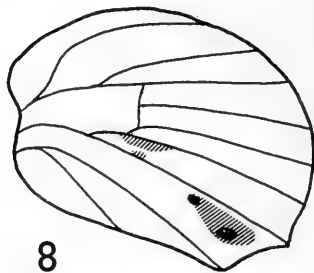
*Figure C:* Frequencies with which different wing markings were affected by homoeosis (27 specimens, 36 affected wings)



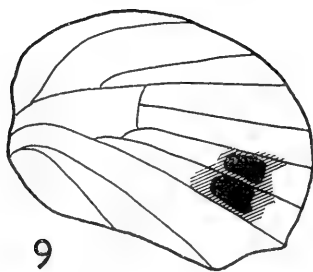
Figures 1-6: Unilateral underside homoeosis in *Lycaena phlaeas*. For full data see List of Specimens



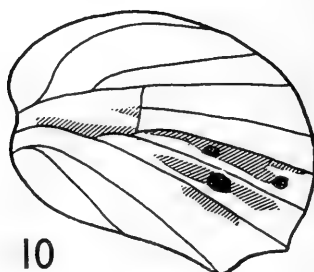
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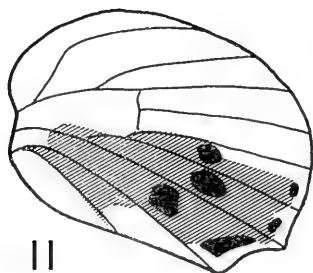
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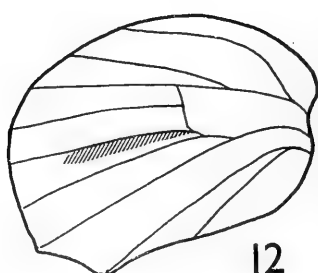
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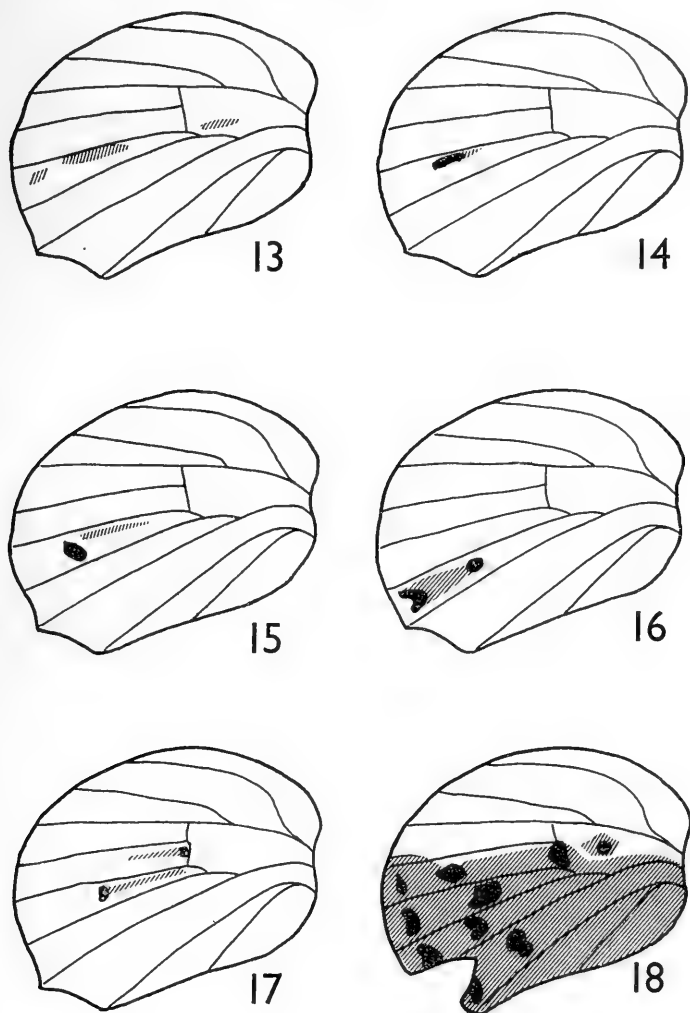


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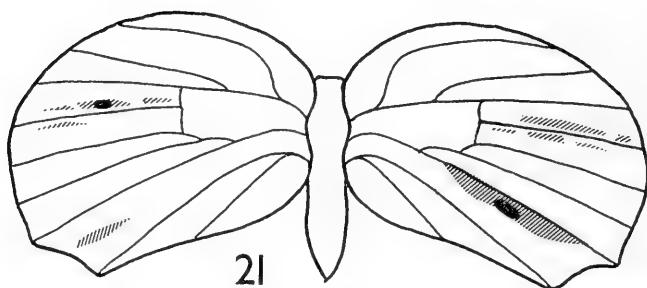
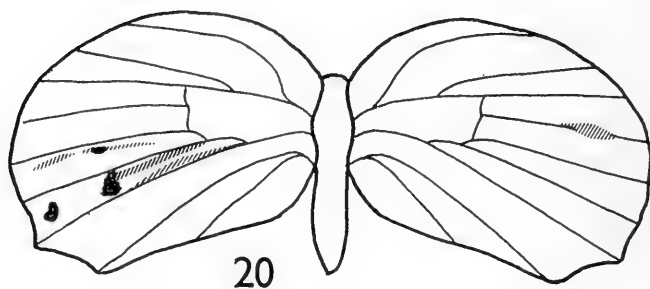
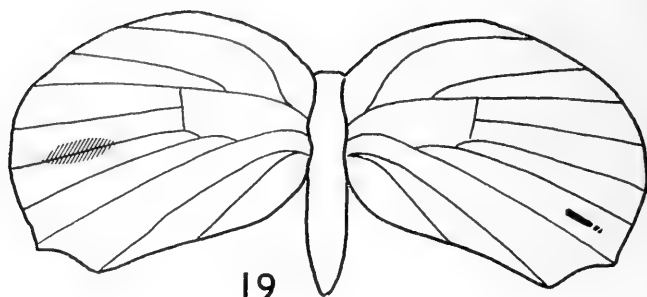


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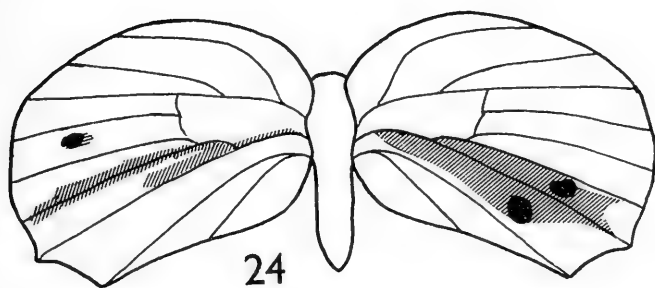
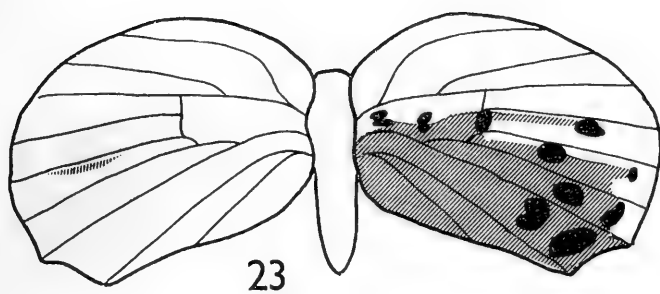
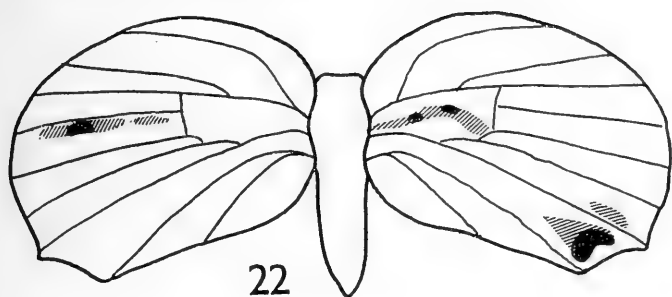
Figures 7-12: Unilateral underside homoeosis in *Lycaena phlaeas*. For full data see List of Specimens



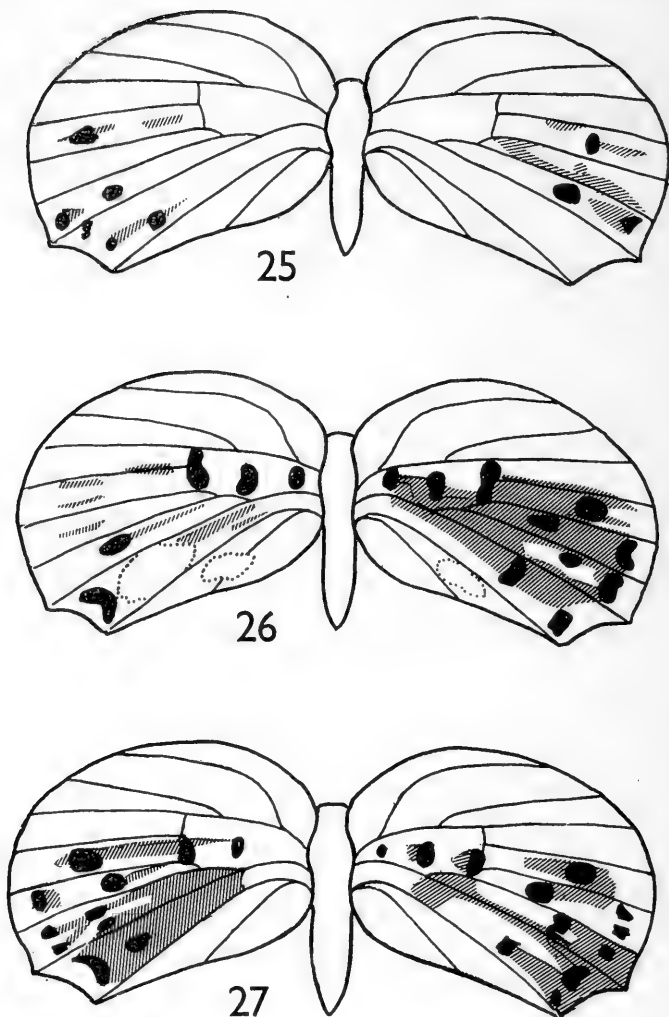
Figures 13-18: Unilateral underside homoeosis in *Lycaena phlaeas*. For full data see List of Specimens



Figures 19-21: Bilateral underside homocosis in *Lycaena phlaeas*. For full data see List of Specimens



Figures 22-24: Bilateral underside homoeosis in *Lycaena phlaeas*. For full data see List of Specimens



Figures 25-27: Bilateral underside homoeosis in *Lycaena phlaeas*. For full data see List of Specimens

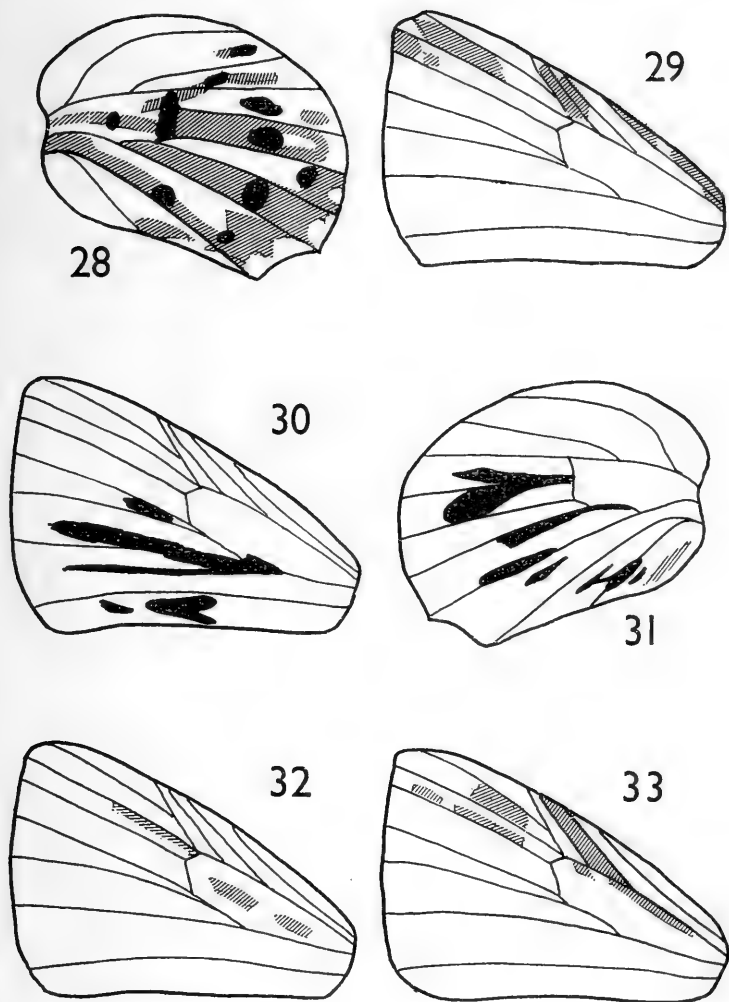
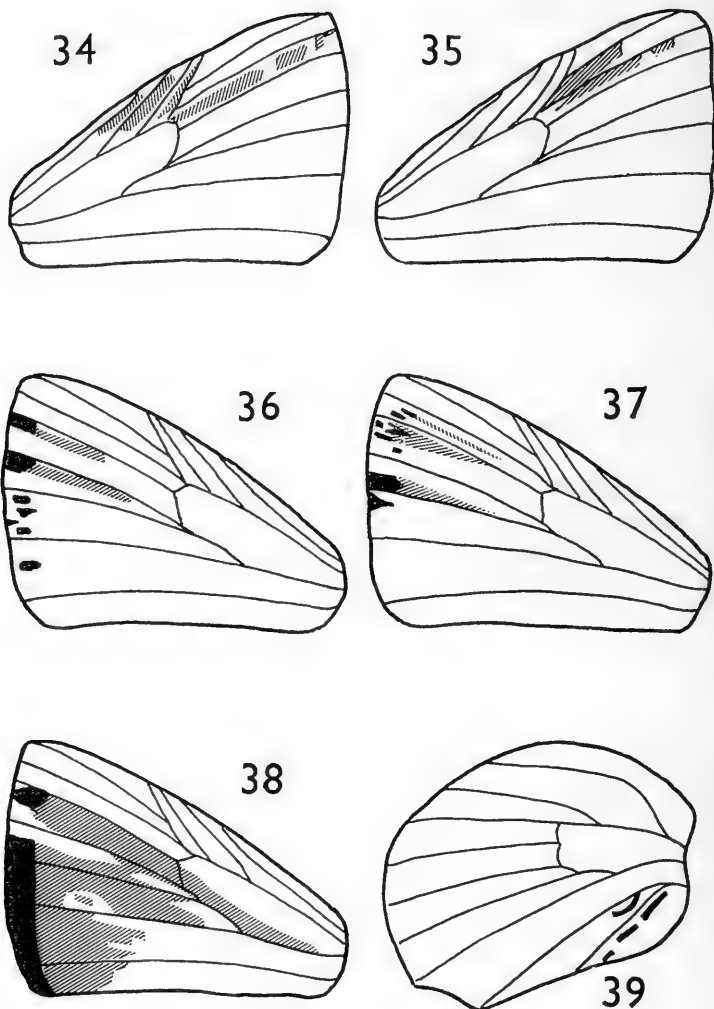


Figure 28: Unilateral upperside homoeosis; Figures 29-31: Unilateral upperside heteromorphosis; Figures 32-33: Unilateral underside heteromorphosis in *Lycaena phlaeas*. For full data see List of Specimens.



Figures 34-39: Unilateral underside heteromorphosis in *Lycaena phlaeas*. For full data see List of Specimens.

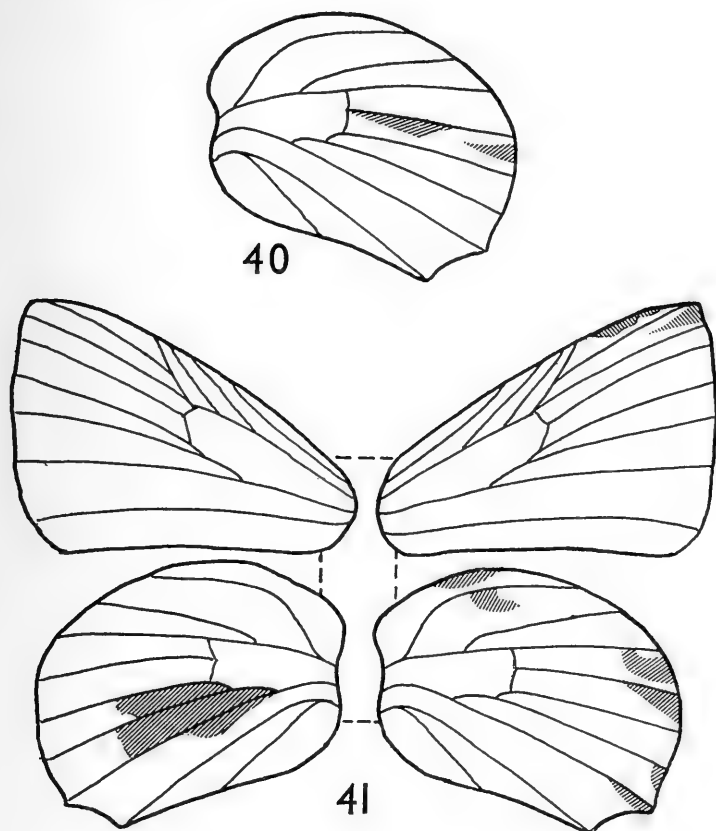
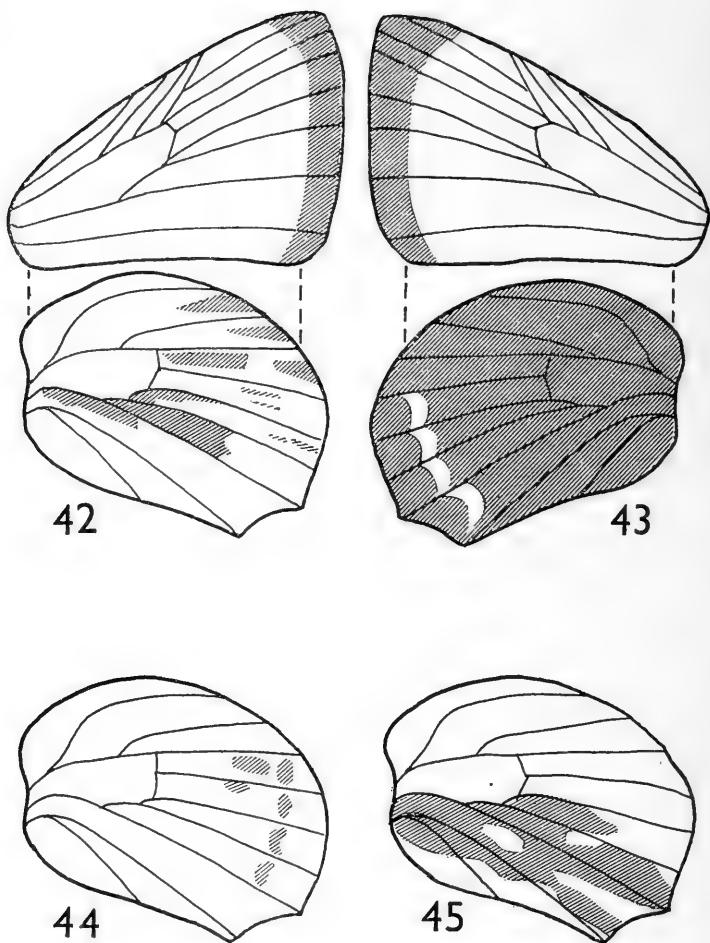


Figure 40: Unilateral underside heteromorphosis in *Lycaena phlaeas*; Figure 41: Bilateral underside heteromorphosis in *Lycaena phlaeas*. For full data see List of Specimens.



*Figures 42 & 44: Unilateral heteromorphosis; Figure 43: Bilateral heteromorphosis; Figure 45: Underside with pale areas in Lycaena phlaeas. For full data see List of Specimens.*

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